AMAZONIANA XV (1/2): 35 - 50 Kiel, Dezember 1998

Relation between flood pulse and functional composition of the macroinvertebrate benthic fauna in the lower Rio Negro, Amazonas, Brazil

by

J.L. Nessimian, L.F.M. Dorvillé*, A.M. Sanseverino** & D.F. Baptista*

Dr. J.L. Nessimian, M.Sc. L.F.M. Dorvillé & M.Sc. A.M. Sanseverino, Departamento de Zoologia, Instituto de Biologia, UFRJ, Caixa Postal 68044, 21944-970, Rio de Janeiro, RJ, Brazil.
Dr. D.F. Baptista, Departamento de Biologia, Instituto Oswaldo Cruz, FIOCRUZ, Av. Brasil 4365, Manguinhos, 21045-900 Rio de Janeiro, RJ, Brazil.
(Accepted for publication: June, 1998).

Abstract

In a twelve-month study carried out at the archipelago of Anavilhanas, lower Rio Negro, State of Amazonas, Brazil, the macroinvertebrate fauna was sampled from the margins of a lake (Redondo lake) permanently connected to the river. The total biomass of the macroinvertebrates sampled during this period was 9,985.5 mg (dry weight) and 19,314 specimens were collected. Decapods (52.9 %) were the most important group regarding biomass while dipterans (21.1 %), ostracods (20.0 %), cladocerans (14.0 %), and oligochaetes (13.4 %) were the most abundant macroinvertebrates. All taxa showed frequency variations related to the high-low water cycle of Rio Negro and the substrate at the lake margins varied in quantity as well as in composition and structure. The greatest amounts of litter occurred in the flood period, with a higher proportion of new and whole leaves. The degree of litter fragmentation increased towards the low water period. The functional structure of the macroinvertebrate community showed adaptation to the available substrate in each season. A gradient of dominance between the functional categories, related to the distance from the central area of the water body, was observed. Shredders were sampled mainly inside the "igapó" (high water period), in a similar proportion to collectors. On the other hand, collectors were clearly predominant in the dry period. Scrapers were limited to the rising and falling water periods. The same trend is probably found in all the corresponding sections of the Rio Negro.

Keywords: **Flood Pulse Concept, aquatic insects, benthic macroinvertebrates, tropical rain forest, Rio Negro, Amazonia.**

*Programa de Pós-graduação em Zoologia, UFRJ
**Programa de Pós-graduação em Ecologia, UFRJ

ISSN 0065-6755/1998/035/ © MPI für Limnologie, AG Tropenökologie, Plön; INPA, Manaus

Introduction

The influence of the areas adjacent to the rivers on their biota became important in ecological studies since the approaches of ODUM (1957) and MARGALEF (1960). CUMMINS (1974) and WALLACE et al. (1977) considered the structure and function of freshwater communities to be regulated by biotic and environmental factors. Recent studies on the structure and function of biological communities of rivers regard the river as an open ecosystem dependent from the neighbouring areas, especially in the riverine zones. The results of these works have provided many debates about the more appropriate models to understand the energy flow of these water bodies.

VANNOTE et al. (1980) developed the River Continuum Concept (RCC), which considers the river as a longitudinal continuum gradient of physical conditions, with the corresponding adjustment of the biota to the dominant aspects in each order. This fauna would be structured, in a certain reach, to increase the utilization of the resources not consumed upstream. This model was tested in several rivers and received some modifications posteriorly. Due to the restriction of its applicability to small and medium streams, other models were developed. Among them is the Flood Pulse Concept of JUNK et al. (1989), JUNK (1997a, b), for large rivers with adjacent flood areas. In this model the flood pulse is the main factor governing the productivity of the river floodplain system. So, there is an interdependence between the river and the adjacent flood area (transversal to the axis of the river), regardless of the RCC processes (longitudinal orientation). In this environment, the benthic fauna represents perhaps the most effective component in the energy flow between the aquatic and terrestrial compartments.

Many studies about the fauna of aquatic macroinvertebrates in flooded areas in Amazonia have revealed a great variety of adaptations to the flood pulse (e.g. IRMLER 1975, 1979; REISS 1977; KENSLEY & WALKER 1982; WALKER & FERREIRA 1985; NESSIMIAN 1985) and energy flow (WALKER et al. 1991).

Our aim is to interpret the flood pulse in a blackwater river (Rio Negro) by means of a functional approach of the benthic macroinvertebrate fauna collected at the margins of a lake, constantly connected to the river. It is also our goal to find out the adjustments to the environmental changes displayed by this community.

Study area

This work was conducted at the Estação Ecológica de Anavilhanas (Ecological Station of Anavilhanas), in the archipelago of Anavilhanas, Rio Negro, State of Amazonas, Brazil (between 2° and 3°S and 60° and 61°W). In this section, the river shows an annual variation of water level of 10 m in average, submerging completely the islands during the flood period (May-August in 1981 and as of April in 1982). The Rio Negro is a typical blackwater river, with acid waters (pH between 3.7 and 5.5) and conductivity values ranging from 6.3 $\mu S \cdot cm^{-1}$ to 12.1 $\mu S \cdot cm^{-1}$ (REISS 1977; LEENHEER & SANTOS 1980). The water transparency varies from 1.3 m to 2.3 m. It has a poor phytoplankton flora and the concentration of dissolved oxygen is between 4 $mg \cdot l^{-1}$ and 7 $mg \cdot l^{-1}$ (IRMLER 1975). Dissolved organic acids are present in significant amounts, being the humic and fulvic acids 44 % and 8 %, respectively (LEENHEER 1980). During the flood periods precipitation of humic acids occurs in the "igapós", forming a gelatinous layer over the litter (IRMLER 1975, 1979; WALKER 1992).

The vegetation of the islands is characterized by flood forests (seasonal "igapó" *sensu* PRANCE 1980), very similar to the vegetation of lower "igapó" (ADIS 1984; REVILLA 1981; TAKEUCHI 1968), the higher parts being in a climax condition (RODRIGUES 1961). Most of the plant species display marked periods of leaf production and fall. The period of highest litter production is during the flood months, the maximum being in July (REVILLA 1981; ADIS et al. 1979; WORBES 1997).

Material and methods

Sampling was performed in the Lago Redondo (Redondo lake), also known as Lago do Prato, with an approximate surface area of 3 km^2 during low water, constantly open, with an entry and an exit connecting it to the river. The lake follows the changes in water level of Rio Negro during the whole year. The selected site has a slight slope, allowing continuity of sampling at the margins during the entire cycle of water level fluctuations.

Fifteen samples were taken monthly, from a 3 m section at the moving margin, following the hydrologic cycle of the river, from May 1981 to April 1982, with a D-shaped net (mesh size: 1 mm; dimensions: 30 cm in length, 25 cm in height, 15 cm in depth). Despite the mesh size, an obliterating effect caused by the nature of the substrate allowed the gathering of animals smaller than 1 mm. Each sample represented about 0.75 m^2 of the ground. In this study the total data obtained per month were considered (NESSIMIAN 1985).

The collected material was preserved in 70 % ethanol and separated in two levels: larger or smaller than 1 mm. The material smaller than 1 mm was counted by the two-stage method (ELLIOTT 1977). Counting and identification were made by means of a stereoscopic microscope with a maximum amplification of 40x. Specimens were identified to the highest possible taxonomic level or to morphospecies, with the aid of general keys and/or specialists.

Biomass was measured by weighing the fixed material with an analytical balance with 1 mg precision. Mean values obtained for morphospecies groups were used. The conversion to dry weight was made by the factor 0.2 (WINBERG 1971). Molluscs and caddisflies were weighed without their respective shells and cases. Functional trophic categories were assigned according to the classification proposed by MERRITT & CUMMINS (1984), and using the observations of KENSLEY & WALKER (1982), NESSIMIAN (1985), and WALKER (1988, 1995). Taxa belonging to more than one category had their biomass values equally distributed among them, except for observed preferences. The collector-gatherers category (fine particulate organic matter - FPOM <1 mm) was divided in macrocollectors (FPOM >0,5 mm) and microcollectors (FPOM <0,5 mm).

Monthly means of water level for the Rio Negro during the period of this study were obtained at the harbour of Manaus, AM.

The organic material (litter) present in the samples was previously dried at 105 °C and then quantified by weighing with an analytical balance with 0.1 mg precision. The composition of the litter (leaves, twigs etc.) was obtained through the measurement of the area occupied by each of its components in a plain surface. The degree of litter integrity was evaluated by the number of objects (leaves, leaf fragments etc.) crossed by transect lines of fixed distance, over the material disposed on a plane surface.

Significant variations in total and percentage values of frequency and biomass among the months were checked by means of the Chi-square test for all the functional categories (ELLIOTT 1977). Differences in biomass were also analysed by the Chi-square test (contingency table) and by the cluster analysis (UPGMA method; SNEATH & SOKAL 1973) using the MORISITA-HORN index (ELLIOTT 1977). The MARGALEF index of richness (LUDWIG & REYNOLDS 1988) was used to compare the fauna collected between months.

Results

The water level ranged from 17.3 m (November 1981) to 27.9 m (May 1982). The flood of 1981 exhibited a maximum value of 26.7 m (June). The substrate of the lake margins varied in quantity as well as in composition and structure during the sampling period. The greatest amounts of litter occurred during flooding (May-August 1981 and as of April 1982). Litter composition varied little (Fig. 1), with leaves being the major component. The lowest quantities of this item were recorded during the fall of the water level. Fragmentation of the litter increased towards the lowering of the waters, with younger and whole leaves observed during the flood (Fig. 1).

The total biomass of macroinvertebrates collected at the margins of Lago Redondo was 9,985.5 mg (dry weight) for a total of 19,314 specimens distributed in 125 morpho-species. Decapods (52.9 %) were the most important group regarding biomass, while dipterans (21.1 %), ostracods (20.0 %), cladocerans (14.0 %) and oligochaetes (13.4 %) were the most abundant. The total biomass of macroinvertebrates showed a significant change during this study with peaks at the lowering of the waters (Sept., highest), at the lowest water level (Nov.), and at the rising waters (Fig. 2).

The distribution of the taxa among the trophic functional categories and their main periods of occurrence are given in Table 1. The majority of species was present in the seasonal "igapó". They showed no or little feeding specificity, but used a wide variety of resources according to availability.

Significant variations were found both in biomass and in frequency of the functional categories (Fig. 3). This was also true in relation to the percentage of frequency and biomass over the sampling period (except for the biomass of piercers-herbivores and filterers) following the cycle of high-low water level, consequently leading to changes in the composition of the macroinvertebrate community (Fig. 4). The value obtained in the Chi-square test (contingency table) regarding the community composition in terms of biomass of the several functional categories was highly significant ($p = 0,0000$). The collectors (macrocollectors, microcollectors and filterers) formed the dominant group, followed by the predators. The shredders were found mainly at the seasonal "igapó". The scrapers showed a single peak (August, 1981; receding waters) but their percentage was also important at the beginning of the rising water level. Piercers-herbivores represented the group with the smallest contribution.

Three groups of community structures were distinguished by means of cluster analysis (Fig. 5). The communities of the low water months (November and December, 1981) differed in a higher extent from the remaining ones, showing a dominance of microcollectors. The other two groups represented the flood period (May-August 1981 and as of April 1982) with a higher contribution of predators and a balance between the other categories, and the periods of rising and falling water level (January-March 1982 and September and October 1981, respectively) with a dominance of macrocollectors. The rising water months presented also an increase in the participation of shredders. Higher values of community richness were found during the rising waters and during flooding months while the lowest values were recorded during low water level (Table 2).

Discussion

The results presented herein support previous studies about the importance of the seasonal "igapó", and above all, of the substrate (litter) for the macroinvertebrate benthic fauna (REISS 1977; IRMLER 1975, 1979; NESSIMIAN 1985; WALKER 1988). The majority of the collected species was found in the seasonal "igapó", closely associated to the litter (food, shelter, and breeding site). As pointed out by IRMLER (1975), JUNK (1978), KENSLEY & WALKER (1982), and WALKER & FERREIRA (1985), these are opportunistic species (presenting "r" selection), with high reproductive rates, fast development, and a life history adjusted to the hydrologic cycle of the river. *Brasilocaenis irmleri* (Caenidae), for instance, completes its post-embryonic development within 14 days (NOLTE 1988). NESSIMIAN (1985) observed first instars of several species of Insecta (Ephemeroptera, Odonata, and Coleoptera), as well as off-spring production in Decapoda, Gastropoda, Oligochaeta, and Hirudinea at the period of rising water level. The seasonal "igapó" was also assigned as a breeding site for Decapoda by WALKER & FERREIRA (1985).

The main channel of the Rio Negro and the central area of the lakes at Rio Negro floodplain show a much lower abundance and richness of species than their respective margins. This is especially true for the benthos, which often represents nearly the whole productivity of the water body (REISS 1977; IRMLER 1979; JUNK et al. 1989). In general, the biota is more concentrated at the margins and hence, the faunas of these sites better represent the status of the biota in this environment. In this way, the dominant biotic function displayed in a certain reach of a river or in a lake during a certain time is mainly represented by the biotic function dominant at the margins. There are many factors accounting for this difference, *e.g.* depth, light, dissolved oxygen, flow, and substrate.

WALKER (1995) calls attention that in the seasonal "igapó" the space and not the resource is the limiting factor for the benthic fauna, even if resources of poor quality, as noted by JUNK et al. (1989) and JUNK (1997a, b). On the other hand, in the main river channel and in the central zone of the blackwater lakes, besides other unfavourable conditions, the paucity of available resources act as a limiting factor. Thus, with the expansion of the littoral zone into the seasonal "igapó", there is an associated expansion of the benthic fauna. Retraction and concentration occur during the receding waters.

When JUNK et al. (1989) proposed the Flood Pulse Concept for rivers with flood areas in contrast to the River Continuum Concept of VANNOTE et al. (1980) they assembled many of these observations and assigned, among other flood areas, the seasonal "igapó" as an aquatic-terrestrial transitional zone (ATTZ). The seasonal "igapó" is an integrant part of the river and provides energy to maintain its biota, regardless of the material derived from the upstream processes. The biomass curve (Fig. 2) and the number of species in each month (Table 2) correspond with the predicted model of the Flood Pulse Concept. The highest amount of organic matter and species richness occurred inside the seasonal "igapó", while the highest biomass values are found at the margins of the seasonal "igapó", even taking into account a concentration of the fauna during the falling waters. Even being a blackwater system (low primary productivity), the presence of scrapers, filterers, and piercers-herbivores indicates the largest primary productivity during the periods of rising and falling waters, at the margins of the seasonal "igapó", where there is more light.

The flood pulse and the moving littoral provide a qualitative shift in the substrate, and hence, changes in the kind of resource available to the aquatic biota. Even with some plasticity in resource utilization at the species level, there is an adjustment of the community, with species replacement and changes in the functional organization. The groups depicted in the dendrogram of Figure 5 are consistent with the four hydrologic periods of the flood pulse, and more specifically with the nature of the substrate, that is, higher or lower amount of litter, degree of its fragmentation, and the presence of algae (Fig. 1). The dominance of a functional group seems to be directly correlated with these factors. For the predators however, the most important factor should be the number of organisms (preys). This group showed an increase during the receding waters and at the period of low water.

A transversal gradient to the water body can be observed in relation to the composition and structure of the substrate, as well as in the functional structure of the fauna, both regulated by the flood pulse. The same gradient should be found in all the corresponding sections of the Rio Negro, with a temporal change of the functional organization.

This functional gradient may be compared to a continuum system like that of VANNOTE et al. (1980), with the structure of the fauna changing according to its position in the river channel (Figs. 4 and 6). The values of the MARGALEF richness index support this comparison (Table 2). Therefore, concerning the structure of the macroinvertebrate fauna, the flood period (when the margins are within the igapó forest) resembles the lower orders of a stream, both with a great influence of the surrounding vegetation (temperature, light, and feeding resource). Except for the predators, the highest numbers of shredders and macrocollectors are recorded during this period. The periods of falling and rising waters are similar to the intermediate stream orders (3^{rd} to 5^{th} orders according to each river), which represent a transitional zone in the longitudinal gradient. In these periods the margins are out of the igapó forest and at the real limits of the river (here called "border zone"). In an analogous way, the dominant fauna in those periods occupy an intermediary position in the river flood plain, between the river and the forest. In both periods there is more light and more temperature variation, with higher numbers of macrophytes and algae present (REISS 1977; NESSIMIAN 1985). Besides that, there is less litter from the forest and its fragmentation is higher. A dramatic decrease in shredders and an increase in macrocollectors, scrapers and piercers-herbivores is also recorded. The highest species richness was observed at the rising water period (seasonal "igapó" margin), as found in the 3^{rd} to 5^{th} stream orders. During the period of lowest water level, in which the littoral retracts to the original river channel, the benthic macroinvertebrate community resembles higher orders of a stream (>5^{th} orders). The organic material available in the substrate is very particulated and a higher contribution of microcollectors and herpobiont filterers is recorded, as well as a complete absence of shredders.

Probably, functional gradients should take place in relation to the flood pulse, in all flooded areas. However, due to the peculiar aspects of the blackwater rivers, similar studies are necessary in "várzea" areas (whitewater rivers) in order to check for the existence of similar gradients.

Resumo

Em estudo realizado no Arquipélago de Anavilhanas, baixo Rio Negro, Amazonas, no período de 12 meses, foi feita amostragem da fauna de macroinvertebrados das margens de um lago permanentemente conectado ao rio (Lago Redondo). A biomassa total de macroinvertebrados coligidos durante o período amostral foi de 9.985,5 mg (peso seco) para um total de 19.314 indivíduos. Decápodes (52,9 %) foram os mais importantes em termos de biomassa enquanto que dípteros (21,1 %), ostrácodos (20,0 %), cladóceros (14,0 %) e oligoquetos (13,4 %) foram os mais abundantes. Todos os táxons apresentaram variações de freqüência relacionadas ao ciclo de cheia e vazante do rio Negro e o substrato nas margens variou tanto em quantidade como em composição e estrutura.

As maiores quantidades de serrapilheira ocorreram no período de cheia, com maior participação relativa de folhas mais novas e inteiras. O grau de fragmentação do "litter" aumentou em direção à vazante. A estrutura funcional da fauna de macroinvertebrados apresentou-se adaptada ao substrato disponível em cada estação. Observou-se um gradiente de dominância entre as categorias funcionais em função da distância da área central do corpo d'água. O mesmo gradiente deve repetir-se para todo o trecho correspondente do rio Negro. Fragmentadores ocorreram principalmente no igapó (período de cheia) com participação relativa semelhante à dos coletores. O período de seca apresentou dominância nítida de coletores. Raspadores tiveram participação limitada aos períodos de início de subida e descida do nível de água.

Acknowledgments

The first author thanks Dr. Ilse Walker (INPA) for the valuable suggestions and supervision during the field work. The following researchers identified part of the studied material: Prof. Dr. Célio Magalhães (INPA) - Decapoda; Prof. Dr. Alcimar L. Carvalho (Museu Nacional, UFRJ) - Odonata; Prof. Nélson Ferreira Jr. (Instituto de Biologia, UFRJ) - Coleoptera; Prof. Elidiomar R. da Silva (UNIRIO) - Ephemeroptera; Aline S. Vargas and José Ricardo I. Ribeiro (Instituto de Biologia, UFRJ) - Hemiptera. Prof. Dr. Otávio S. Pieri (FIOCRUZ) revised the english text. This work was supported by the following institutions: CNPq, FAPERJ, FUJB and CEPG-UFRJ.

References

ADIS, J. (1984): "Seasonal Igapó" - Forests of Central Amazonian Black-Water Rivers and their terrestrial Arthropod Fauna. - In: SIOLI, H. (ed.): The Amazon - Limnology and Landscape ecology of a mighty tropical river and its basin. - W. Junk, Dordrecht: 245-268.

ADIS, J. FURCH, K. & U. IRMLER (1979): Litter production of a Central Amazonian blackwater inundation forest. - Tropical Ecology **20**(2): 236-245.

CUMMINS, K.W. (1974): Structure and function of stream ecosystems. - Bioscience **24**: 631-641.

ELLIOTT, J.M. (1977): Some methods for statistical analysis of samples of benthic invertebrates. - Freshwater Biological Association, London, Scientific Publication **25**: 160 pp.

IRMLER, U. (1975): Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazonia. - Amazoniana **5**(3): 337-409.

IRMLER, U. (1979): Considerations on structure and function of the "Central Amazonian inundation forest ecosystem" with particular enphasis on selected animals. - Oecologia **43**: 1-18.

JUNK, W.J. (1997a): General Aspects of Floodplain Ecology with Special Reference to Amazonian Floodplains. Ecology of a Pulsing System. - In: JUNK, W.J. (ed.): The Central Amazonian Floodplain. Ecology of a Pulsing System. Springer Verlag, Berlin: 3-20.

JUNK, W.J. (1997b): Structure and function of the large central Amazonian river floodplains: Synthesis and discussion. - In: JUNK, W.J. (ed.): The Central Amazonian Floodplain. Ecology of a Pulsing System. Springer Verlag, Berlin, Ecological Studies: 455-472.

JUNK, W.J., BAYLEY, P.B. & R.E. SPARKS (1989): The flood pulse concept in river-floodplain systems. - In: DODGE, D.P. (ed.): Proceedings of the International Large Rivers Symposium (LARS). - Can. Spec. Publ. Fish. Aquat. Sci. **106**: 110-127.

KENSLEY, B. & I. WALKER (1982): Palaemonid shrimps from the Amazon Basin, Brazil (Crustacea: Decapoda: Natantia). - Smithsonian Contributions to Zoology **362**: 1-28.

LEENHEER, J.A. (1980): Origin and nature of humic substances in the waters of the Amazon river basin. - Acta Amazônica **10**(3): 513-526.

LEENHEER, J.A. & V. SANTOS (1980): Considerações sobre os processos de sedimentação na água preta ácida do Rio Negro (Amazônia Central). - Acta Amazônica **10**(2): 343-355.

LUDWIG, A.J. & J.F. REYNOLDS (1988): Statistical ecology. A primer on methods and computing. - J. Wiley & Sons, New York: 342 pp.

MARGALEF, R. (1960): Ideas for a synthetic aproach to the ecology of running water. - Int. Rev. Hydrogr. Hydrobiol. **45**: 133-153.

MERRITT, R.W. & K.W. CUMMINS (1984), (eds.): An introduction to the aquatic insects of North America. - Kendall/Hunt Publ., Dubuque: 722 pp.

NESSIMIAN, J.L. (1985): Estudo sobre a biologia e ecologia da fauna invertebrada aquática da liteira submersa das margens de dois lagos no Arquipélago de Anavilhanas, Rio Negro, Amazonas, Brasil. - M.Sc. thesis - INPA/FUA, Manaus, AM: 220 p.

NOLTE, U. (1988): Small water colonization in pulse stable (várzea) and constant (terra firme) biotopes in the Neotropics. - Arch. Hydrobiol. **113**(4): 541-550.

ODUM, H.T. (1957): Trophic structure and productivity of Silver Springs, Florida. - Ecol. Monogr. **27**: 55-112.

PRANCE, G.T. (1980): A terminologia dos tipos de florestas amazônicas sujeitas a inundação. - Acta Amazônica **10**(3): 495-504.

REISS, F. (1977): Qualitative and quantitative investigations on the macrobenthic fauna of Central Amazon lakes. I. Lago Tupé, a blackwater lake on the lower Rio Negro. - Amazoniana **6**(2): 203-235.

REVILLA, J.D.C. (1981): Aspectos florísticos e fitossociológicos da floresta inundável (igapó). Praia Grande, Rio Negro, Amazonas, Brasil. - M.Sc. thesis - INPA/FUA, Manaus, AM: 129 p.

RODRIGUES, W.A. (1961): Estudo preliminar da mata de várzea de uma ilha no baixo Rio Negro, de solo argiloso e úmido. - CNPq/INPA, Série Botânica **10**: 1-50.

SNEATH, P.H.A. & R.R. SOKAL (1973): Numerical taxonomy - the principles and practice of numerical classification. - W.H. Freeman & Co., San Francisco: 573 pp.

TAKEUCHI, M. (1968): The structure of the Amazonian vegetation. VI - igapó. - Journal Fac. Sci. Univ. Tokyo III **8**(7): 297-308.

VANNOTE, R.L., MINSHALL, G.W., CUMMINS, K.W, SEDELL, J.R. & C. CUSHING (1980): The river continuum Concept. - Can. J. Fish. Aquat. Sci. **37**: 130-137.

WALKER, I. (1988): Study of benthic micro-faunal colonization of submerged litter leaves in the central amazonian blackwater stream Tarumã-Mirím (Tarumanzinho). - Acta Limnologica Brasiliensis **2**: 623-648.

WALKER, I. (1992): The benthic litter habitat with its sediment load in the inundation forest of the Central Amazonian blackwater river Tarumã-Mirím. - Amazoniana **12**(2): 143-153.

WALKER, I. (1995): Amazonian streams and small rivers. - In: TUNDISI, J.G., BICUDO, C.E.M. & T. MATSUMURA-TUNDISI (eds.): Limnology in Brazil. - ABC/SBL, Rio de Janeiro: 167-193.

WALKER, I. & M.J.N. FERREIRA (1985): On the population dynamics and ecology of the shrimp species (Crustacea, Decapoda, Natantia) in the central amazonian river Tarumã-Mirím. - Oecologia **66**: 264-270.

WALKER, I., HENDERSON, P.A. & P. STERRY (1991): On the patterns of biomass transfer in the benthic fauna of an amazonian blackwater river as evidenced by ^{32}P label experiment. - Hydrobiologia **215**: 153-162.

WALLACE, J.B., WEBSTER, J.R. & W.R. WIIDALL (1977): The role of filter feeders in flowing waters. - Arch. Hydrobiol. **79**: 506-532.

WINBERG, G.G. (1971): Symbols, units and conversion factors in studies of freshwater productivity. - I.B.P. Central office, London: 23 pp.

WORBES, M. (1997): The forest ecosystem of the floodplains. - In: JUNK, W.J. (ed.): The Central Amazon Floodplain: Ecology of a Pulsing System. - Springer-Verlag, Berlin: 223-265.

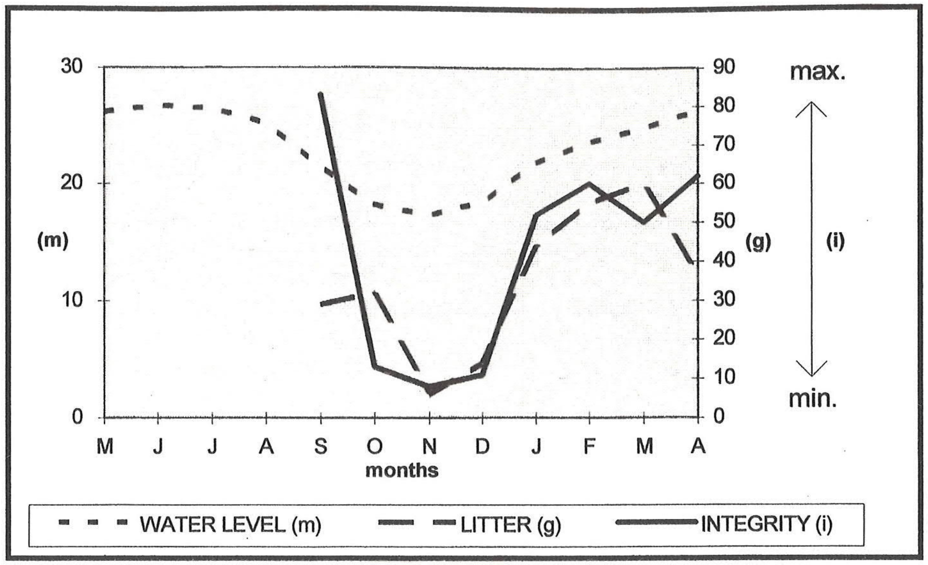

Fig. 1:
Change in the water level of Rio Negro, at Manaus and in the amount of litter and its degree of integrity at the margins of Lago Redondo, archipelago of Anavilhanas (Rio Negro) from May 1981 to April 1982.

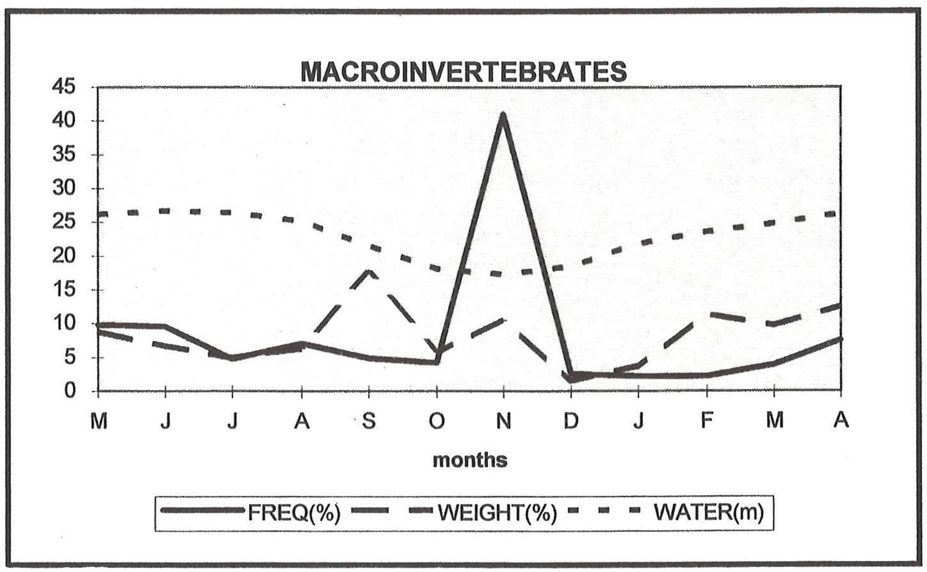

Fig. 2:
Change in the frequency (FREQ) and biomass (WEIGHT) of the macroinvertebrate fauna at the margins of Lago Redondo, archipelago of Anavilhanas (Rio Negro) from May 1981 to April 1982. Values are given as percentages of the total amount of frequency and biomass in the sampling period.

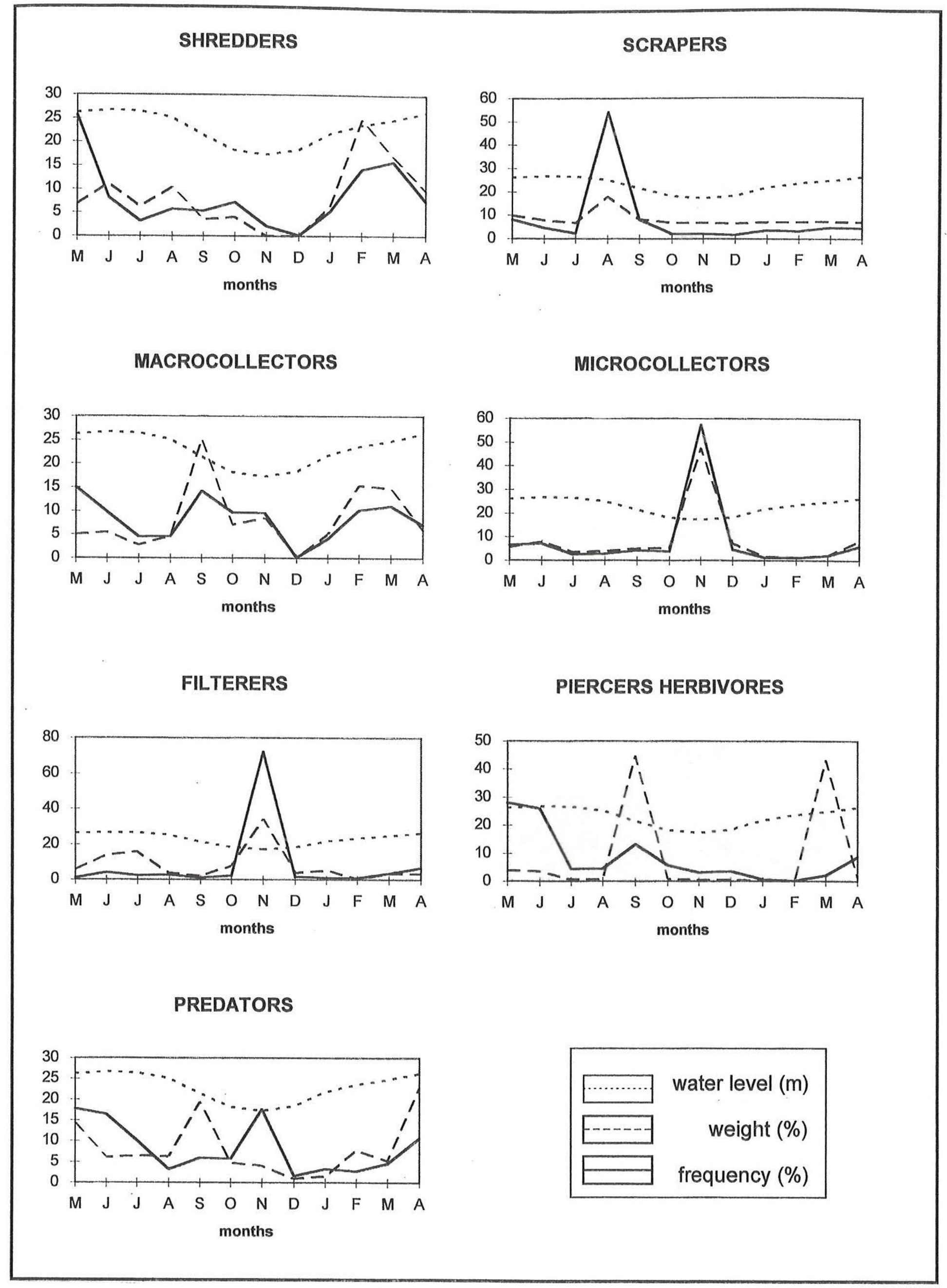

Fig. 3:
Change in the frequency (FREQ) and biomass (WEIGHT) of the several functional categories of the macroinvertebrate fauna collected at the margins of Lago Redondo, archipelago of Anavilhanas (Rio Negro) from May 1981 to April 1982. Values are given as percentages of the total amount of frequency and biomass for each category in the sampling period.

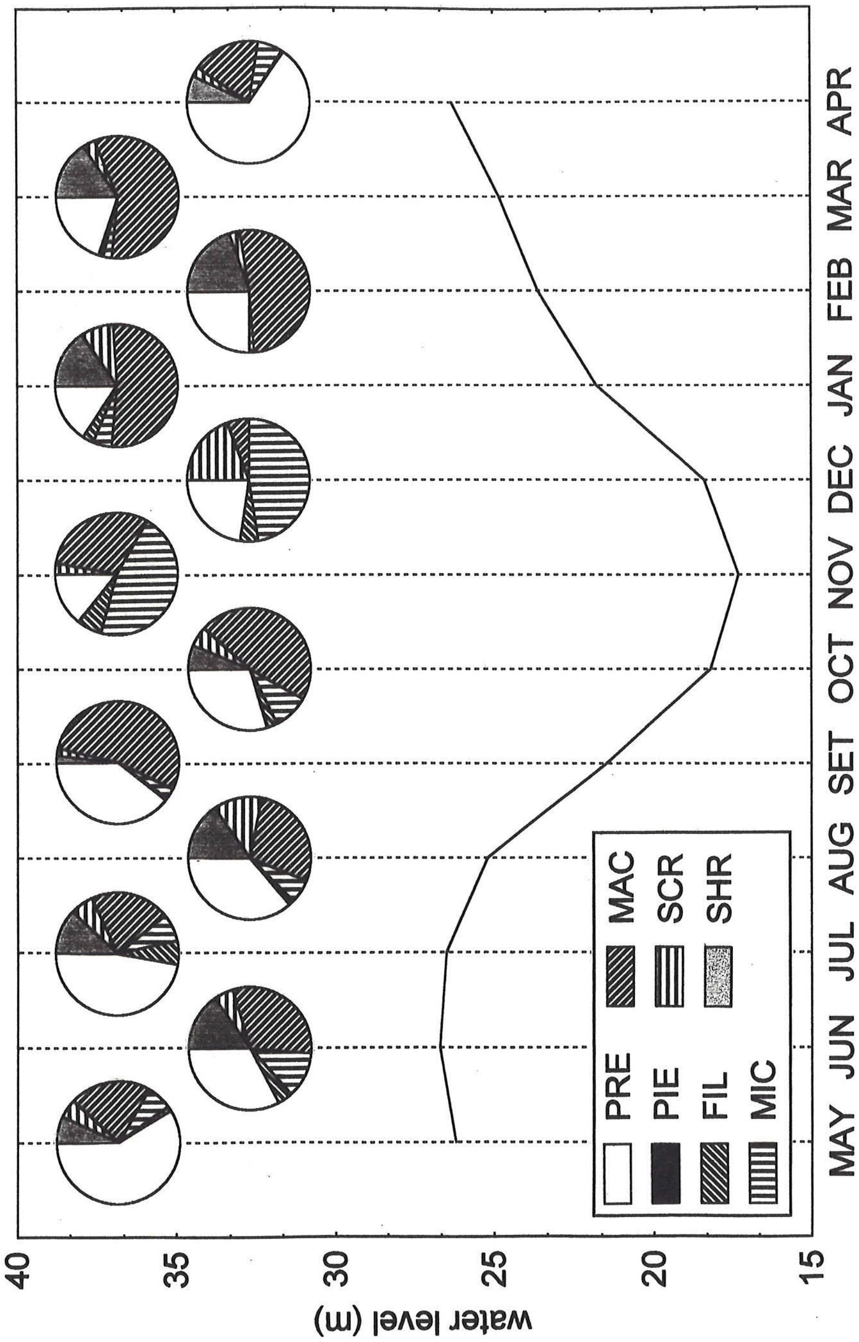

Fig. 4:
Change in the biomass of the functional categories of the macroinvertebrate fauna collected at the margins of Lago Redondo, archipelago of Anavilhanas (Rio Negro) from May 1981 to April 1982. SHR-shredders; SCR-scrapers; MAC-macrocollectors; MIC-microcollectors; FIL-filterers; PIE-piercers-herbivores; PRE-predators.

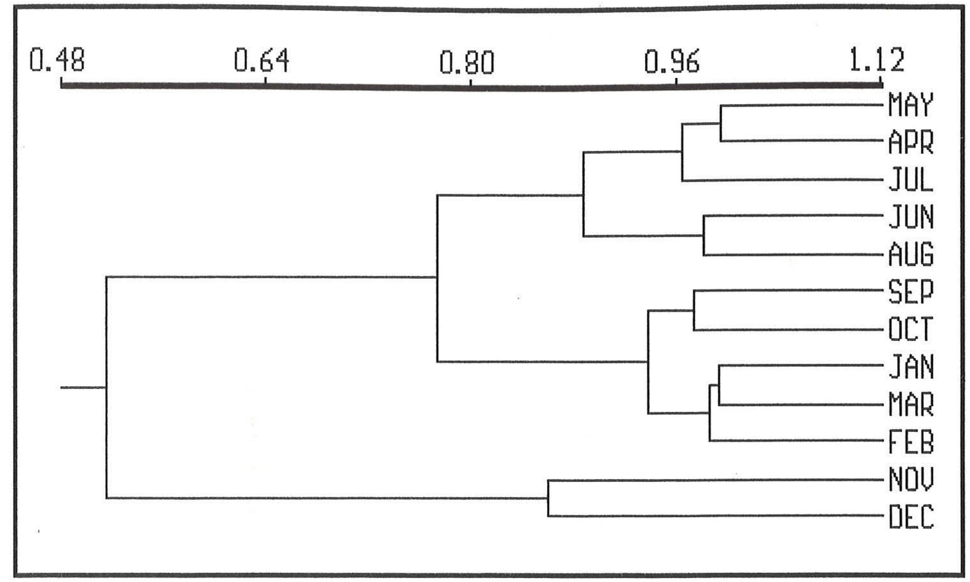

Fig. 5:
Cluster Analysis (UPGMA) based on the Morisita-Horn index calculated from the functional categories of the macroinvertebrate fauna collected at the margins of Lago Redondo, archipelago of Anavilhanas (Rio Negro) for each month (May 1981 to April 1982).

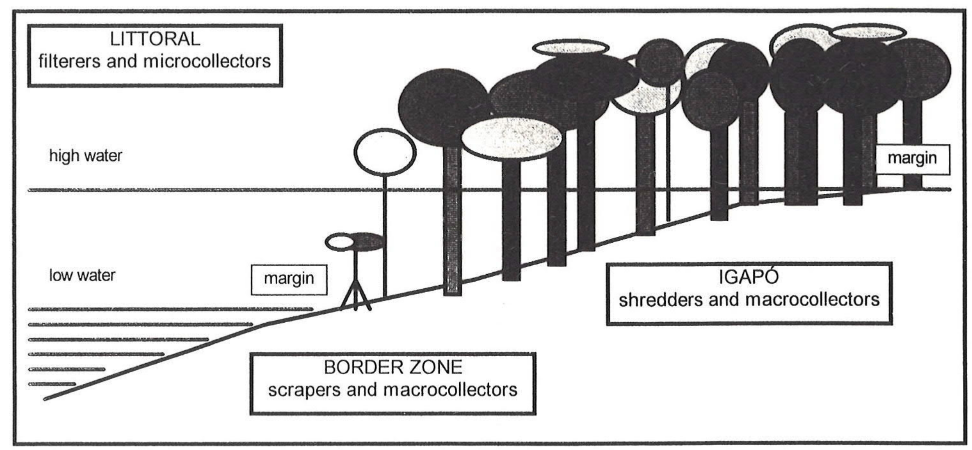

Fig. 6:
Proposed view of the transversal gradient of functional categories at the Rio Negro floodplain.

Table 1: Functional categories and main occurrence periods of the macroinvertebrate taxa sampled at the margins of Lago Redondo (arquipélago of Anavilhanas, Rio Negro) between May 1981 and April 1982. F - falling water; H - high water; L - low water; R - rising water; SHR - shredders; SCR - scrapers; MAC - macrocollectors; MIC - microcollectors; FIL - filterers; PIE - piercers herbivores; PRE - predators. Hyphen indicates continuity.

TAXA	PERIOD	SHR	SCR	MAC	MIC	FIL	PIE	PRE
PORIFERA								
SPONGILLIDAE	R-H-F					X		
TURBELLARIA								
TRICLADIDA	F L							X
TEMNOCEPHALIDA	F							X
NEMATODA	R F				X		X	X
BRYOZOA	H F					X		
GASTROPODA	H-F	X						
OLIGOCHAETA								
NAIDIDAE								
Pristina sp., *Dero* sp.	L				X			
OPYSTOCISTIDAE *Opystocista* sp.	L				X			
LUMBRICIDAE sp.	H			X	X			
HIRUDINEA	F-L							X
GLOSSIPHONIDAE	H							X
ARANEAE	R-H							X
ACARI								
ACTINEDIDA	L							X
ACARI								
ORIBATIDA, GAMASINA	R-H							X
CLADOCERA	L					X		
OSTRACODA	L				X	X		
COPEPODA	R-H				X	X		X
MYSIDACEA *Parvimysis* sp.	H-F			X	X	X		
DECAPODA								
PALAEMONIDAE								
Pseudopalaemon chryseus	F-L	X		X				X
Palamonetes carteri	F	X		X				X
Euryrhynchus amazoniensis	R-H	X		X				X
Euryrhynchus burchelli	R F	X		X				X
TRICHODACTYLIDAE								
Trichodactylus sp.	R-H	X		X				X
Bottiella laevifrons	R-H	X		X				X
DIPLOPODA								
PYRGODESMIDAE	R-H	X						
EPHEMEROPTERA								
CAENIDAE *Brasilocaenis irmleri*	R-H		X	X				
TRICHORYTIDAE *Leptohyphes* sp.	L			X				
BAETIDAE *Baetis* sp.	R		X	X				

Table 1: Continuation

TAXA	PERIOD	SHR	SCR	MAC	MIC	FIL	PIE	PRE
LEPTOPHLEBIIDAE *Ulmeritus* sp.	F		X	X				
POLYMITARCYIDAE								
Astenopus curius	R-H-F	X		X	X			
Campsurus lucidus	F-L			X	X			
ODONATA								
COENAGRIONIDAE	R-H							X
AESHNIDAE *Neuraeschna* sp.	R							X
GOMPHIDAE *Phyllocycla* sp.	L							X
Cyanogomphus sp.	H							X
LIBELLULIDAE *Perithemis* sp., *Micrathyria* sp., *Zenithoptera* sp.	R-H-F							X
HEMIPTERA								
BELOSTOMATIDAE								
Belostoma spp.	R-H							X
NAUCORIDAE	F R							X
NOTONECTIDAE *Notonecta* sp., *Buenoa* sp., *Martarega* sp.	F R						X	X
PLEIDAE *Neoplea* sp.	R-H							X
CORIXIDAE *Tenagobia* sp.	F R						X	
GERRIDAE	H-F							X
VELIIDAE	H							X
TRICHOPTERA								
HYDROPSICHIDAE	F			X	X	X		
LEPTOCERIDAE	R-H-F	X		X	X	X		
POLYCENTROPODIDAE	H-F	X		X	X	X		
CALAMOCERATIDAE	H	X		X	X			
COLEOPTERA								
NOTERIDAE *Suphisellus* sp.	R-H							X
DYTISCIDAE *Laccophilus* sp., *Celina* sp.,	R-H							X
Desmopachria sp., *Pachydrus* sp., *Copelatus* sp.								
GYRINIDAE	L-R							X
HYDROPHILIDAE *Berosus* sp.	H			X				X
ELMIDAE	F R	X	X	X				
HELODIDAE	R-H	X	X	X				
DIPTERA								
CHIRONOMIDAE								
Chironominae	R-H L	X		X	X			
cf. *Stenochironomus* sp.	R-H-F	X						
Orthocladiinae	R-H-F		X		X			
Tanypodinae	R L		X		X			X

Table 1: Continuation

TAXA	PERIOD	SHR	SCR	MAC	MIC	FIL	PIE	PRE
CULICIDAE	R-H-F				X	X		
CERATOPOGONIDAE	L				X	X		
BRACHYCERA	R-H L			X	X			X

Table 2: Number of individuals (N), number of taxa (S) and MARGALEF index of richness (M) for the macroinvertebrate fauna collected at the margins of Lago Redondo, Anavilhanas archipelago (Rio Negro) between May 1981 and April 1982.

MONTHS	N	S	M
MAY	2254	49	6,22
JUNE	2214	49	6,23
JULY	1160	43	5,95
AUGUST	1563	37	4,90
SEPTEMBER	1075	35	4,87
OCTOBER	975	28	3,92
NOVEMBER	9237	28	2,96
DECEMBER	573	15	2,20
JANUARY	506	32	4,98
FEBRUARY	469	37	5,85
MARS	870	53	7,68
APRIL	1720	39	5,10